National Research Council Canada | Conseil national de recherches Canada

Canada

Reprinted from

Canadian Journal of Forest Research

Réimpression du

Journal canadien de recherche forestière

# Second-year shoot development in black spruce *Picea mariana* (Mill.) B.S.P. container seedlings

S. J. Colombo

Volume 16 • Number 1 • 1986

Pages 68–73

Printed in Canada / Imprimé au Canada

# Second-year shoot development in black spruce *Picea mariana* (Mill.) B.S.P. container seedlings

S. J. COLOMBO

*Ontario Tree Improvement and Forest Biomass Institute, Ministry of Natural Resources, Maple, Ont., Canada L0J 1E0*

Received May 28, 1985[1]

Accepted September 30, 1985

COLOMBO, S. J. 1986. Second-year shoot development in black spruce *Picea mariana* (Mill.) B.S.P. container seedlings. Can. J. For. Res. **16**: 68–73.

The relative contributions to 2nd-year shoot elongation by predetermined versus free growth were analyzed for black spruce (*Picea mariana* (Mill.) B.S.P.) seedlings. Seedlings from three hardening regimes, production run, short day, and extended greenhouse, were given various shoot-pruning treatments, from the terminal bud removed to the entire shoot removed except for a lateral shoot at the base. Pruned seedlings were compared with winter-damaged seedlings. Bud flushing was most rapid in short-day seedlings and in pruned seedlings regardless of hardening regime. The capacity for free growth in nonpruned seedlings varied little among seedlings of different hardening regimes, despite large initial differences in bud development between production-run, short-day, and extended greenhouse seedlings. Stem unit length and number of lateral buds per unit of stem length was greater in free growth compared with predetermined growth. Shoot pruning and winter damage had similar effects on shoot growth; the greater the degree of shoot removal, the greater the amount of free growth.

COLOMBO, S. J. 1986. Second-year shoot development in black spruce *Picea mariana* (Mill.) B.S.P. container seedlings. Can. J. For. Res. **16**: 68–73.

La contribution relative de l'élongation de la pousse de la 2e année par la croissance libre versus celle prédéterminée fut analysée chez des semis d'épinette noire (*Picea mariana* (Mill.) B.S.P.). Les semis, soumis à trois cédules d'aoûtement, c'est-à-dire cédule de production, jour court et cédule allongée, ont été élagués suivant divers modes allant depuis l'excision du bourgeon terminal jusqu'à celle de la pousse entière à l'exception d'une pousse latérale à la base. On a ensuite comparé les semis ainsi élagués à des semis ayant subi des dommages hivernaux. Le débourrement fut plus rapide chez les semis jour court et chez ceux qui avaient été élagués, peu importe la cédule à laquelle ils avaient été soumis. Le potentiel de croissance libre chez les semis non élagués a peu varié parmi les semis soumis à diverses cédules, en dépit des différences initiales considerables observées dans le développement des bourgeons entre les semis cédule de production, jour court et cédule allongée. La longueur des verticilles et le nombre de bourgeons latéraux par verticille fut plus grand en croissance libre comparé à la croissance prédéterminée. L'élagage des pousses et le dommage hivernal ont produit des effets similaires sur la croissance de la pousse: la quantité de croissance libre était d'autant plus grande que l'excision de la pousse était importante.

[Traduit par le journal]

## Introduction

The successful establishment of tree seedlings relies in part upon rapid height growth after planting to prevent overtopping by competing vegetation. Early height growth, which is determined by bud and shoot growth characteristics, is especially critical for the establishment of container stock where small initial size and sensitivity to herbicides can exacerbate competition problems. An understanding of bud and shoot growth characteristics of container seedlings is, therefore, important.

Height growth in spruce seedlings is accomplished both by free and predetermined growth. Free growth, as defined by Jablanczy (1971), is the mechanism by which needles are produced *de novo* in the current year rather than from predetermined needles initiated as needle primordia in the previous year's bud. Although free growth is an important contributor to early height growth of tree seedlings (Pollard and Logan 1974), the factors affecting free growth are not well understood.

Free growth in spruce seedlings is also important because of the common occurrence of winter damage, both in nurseries and in the field. Losses of up to 50% of the terminal buds of 1-year-old overwintered black spruce (*Picea mariana* (Mill.) B.S.P.) container or bare-root seedlings have been documented (Colombo and Glerum 1984; Gross 1983). Following terminal bud injury, new shoots will arise from buds lower on the stem. The capacity for free growth will in part determine the ability of tree seedlings to recover from winter damage.

This report documents some 2nd-year shoot growth attributes of black spruce container seedlings. The relative contributions of free growth and predetermined growth to 2nd-year height for shoots originating at different points on the stem are reported.

## Materials and methods

### *Seedling production*

Black spruce seedlings were grown at the Ontario Ministry of Natural Resources Swastika Tree Nursery (48°06′ N, 80°06′ W) using operational procedures for container stock production similar to those described by Carlson (1983). Seeds of a Hearst District general collection (48°47′ to 50°30′ N, 83°25′ to 85°20′ W) were sown May 20, 1981, on a peat moss – vermiculite growing medium (3:1, v/v) in FH408 Japanese paper pots. Seedlings were grown in a plastic-covered greenhouse and on July 23, 8600 seedlings of the crop were assigned to each of three hardening regimes. Additional information regarding these seedlings has been reported previously (Colombo 1982, Colombo and Glerum 1984).

### *Hardening regimes*

Production-run (PR) seedlings were moved outside on August 14, following a 2-week period of reduced nitrogen and increased potassium fertilization. The short-day hardening regime (SD) was similar to that for PR stock, but also employed an 8-h short-day (16-h night) treatment to induce bud initiation, lasting 15 nights prior to the seedlings being moved outside. Extended greenhouse culture (EG) seedlings were fertilized similarly to PR and SD seedlings, but were kept inside a heated greenhouse (minimum temperature, 20°C) until October 1. Minimum temperatures were then progressively lowered until October 21, when the heaters were turned off. EG seedlings were moved outside October 29. All seedlings overwintered at the Swastika Tree Nursery.

[1]Revised manuscript received September 13, 1985.

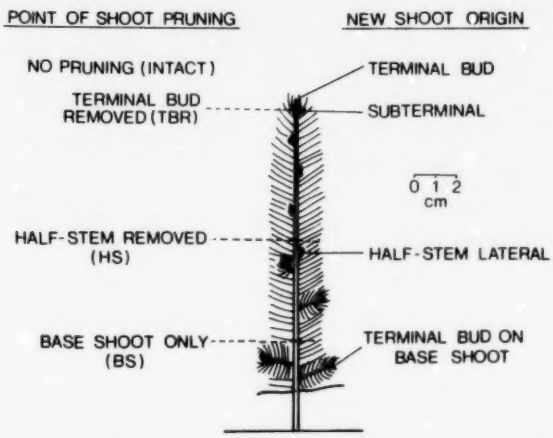


FIG. 1. Shoot-pruning treatments and subsequent origin of new leading shoots in rising 2-year-old black spruce seedlings.

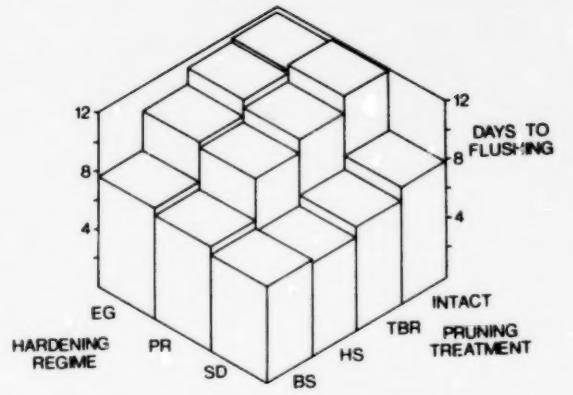


FIG. 2. Number of days to bud flushing in black spruce container seedlings of three hardening regimes with increasing severity of shoot pruning. LSD ($p$ = 0.05) was 1.10 days.

*Bud development*

The number of needle primordia in the terminal buds of 20 randomly selected seedlings of each hardening regime was determined following dissection using the methods of Pollard (1973) and Colombo *et al.* (1982). This number represented predetermined shoot growth.

*Free growth assessments*

To examine the capacity for free growth from buds at different points on the stem, two randomly selected trays totalling about 600 seedlings of each hardening regime (a total of six trays) were placed in a greenhouse (16-h day length, 20–30°C, water as required) in April 1982 and approximately 150 seedlings (one-quarter of each tray) per hardening regime were subjected to one of four shoot pruning treatments (Fig. 1). Treatments were as follows: (*i*) intact (not pruned); (*ii*) terminal bud excised using tweezers (TBR); (*iii*) upper half of the stem removed leaving the lower half of the stem intact (HS); (*iv*) the entire terminal shoot more than 1 cm above the cotyledons removed leaving only a few basal shoots (BS). Seedlings were sampled randomly without blocking as seedling uniformity within trays was high.

Twenty randomly selected seedlings of each treatment were observed during bud flushing and height growth. Bud flushing of the leading shoots was scored according to the following scale: 1, dormant; 2, swollen; 3, bud scales broken; 4, expanding "broom" of needles; 5, new shoot elongating.

Free growth from terminal buds was estimated as the difference between the average number of needle primordia in the 1st-year bud as determined by dissection versus the final number of needles counted on the 2nd-year shoot of 15 randomly selected seedlings of each treatment following bud set in August 1982. Stem unit length and the number of buds per centimetre of stem length were determined after measuring new shoot length and counting the number of lateral buds on the 2nd-year shoot.

The effects of winter damage on shoot growth were examined in PR seedlings only, because there was an insufficient number (<1%) of damaged SD and EG seedlings to allow study. PR seedlings in which about 50% of the main stem was killed were compared with PR seedlings of the HS shoot-pruning treatment. Significantly different treatment means were identified using the LSD test ($p$ = 0.05) following one-way analysis of variance.

## Results

New leading shoots arose at characteristic points on the stem as dictated by the pruning treatment (Fig. 1). For seedlings of the intact treatment, leaders arose from the terminal bud; for the TBR treatment, the leader came from a subterminal lateral bud. With the HS treatment the new leader originated from a lateral bud on the stem within about 1 cm of the cut. In some cases this bud was on a short lateral shoot (Colombo 1984). For the BS treatment, the new leader came from a terminal bud on a lateral shoot.

*Bud flushing*

Bud flushing was most rapid in SD seedlings, regardless of the degree of shoot pruning (Fig. 2). For example, the terminal buds of intact SD seedlings flushed on average after 7.8 days, compared with 11.6 days for EG and 11.8 days for PR seedlings.

Buds flushed more quickly with increasing severity of shoot pruning. For PR seedlings, the average number of days to flushing was 11.8 for the intact treatment, compared with 10.7, 9.8, and 7.2 days for the TBR, HS, and BS treatments, respectively. Lateral buds of the TBR treatments flushed more quickly than lateral buds of the intact treatment.

*New shoot length*

Average new shoot lengths were in all cases shorter for PR seedlings than for either SD or EG seedlings (Fig. 3). The shoots of EG seedlings were the longest, with few exceptions.

New leading shoots of both SD and EG seedlings were in most cases about the same length when the shoot arose from a half-stem bud or from a bud on a basal shoot. In the case of TBR treatments of both those hardening regimes, new leading shoot length was considerably less than in seedlings of the other shoot-pruning treatments. In SD seedlings, leading shoot length was greater for HS and BS than for intact and TBR treatments.

*Bud development and free growth*

Terminal buds of PR, SD, and EG seedlings contained an average of 68, 150, and 273 needle primordia following the completion of first-year bud development, respectively. However, at the end of the second growing season, terminal shoots had produced an average of 196, 261, and 391 needles, respectively (Table 1).

*Stem unit length*

Stem unit length tended to be greater the lower the point of origin of the new shoot on the stem (Table 1). For example, in intact SD seedlings, average stem unit length of the terminal shoot was 0.278 mm, compared with 0.281, 0.315, and 0.321 mm for shoots originating from subterminal buds, half-stem buds, and base shoots, respectively. Stem unit length tended to be greater in new leading shoots of the pruning treatments

FIG. 3. New shoot lengths at different points on the stem of intact or shoot pruned 2-year-old black spruce container seedlings. (A) Production run. (B) Short day. (C) Extended greenhouse culture. Values are means ± SE.

TABLE 1. Number of needles, stem unit length, and number of buds per centimetre of shoot length on new shoots arising at different points on the stem of black spruce seedlings, with and without shoot pruning or winter damage

| | Degree of shoot pruning[a] and new shoot origin[b] | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Intact | | | | Terminal bud removed | | | Half of stem removed | | Half of stem winter killed | | Base shoot only, | LSD[c] | | |
| Hardening regime | A | B | C | D | B | C | D | C | D | C | D | D | B | C | D |
| | | | | | | | No. of needles | | | | | | | | |
| PR | 195.9 | 69.5 | 56.9 | 29.3 | 106.8 | 69.9 | 46.7 | 164.1 | 59.3 | 137.3 | 51.5 | 169.1 | 24.3 | 7.9 | 19.0 |
| SD | 260.5 | 108.7 | 85.1 | 71.1 | 179.9 | 99.4 | 73.0 | 267.7 | 139.5 | | | 269.1 | 20.3 | 45.4 | 27.2 |
| EG | 390.7 | 219.7 | 105.9 | 70.9 | 288.9 | 111.1 | 66.1 | 260.1 | 125.7 | | | 255.1 | 31.5 | 24.4 | 28.6 |
| LSD[d] ($p = 0.05$) | 40.6 | 20.2 | 13.9 | 14.9 | 29.7 | 16.6 | 14.6 | 30.5 | 37.2 | | | 27.0 | | | |
| | | | | | | | Stem unit length (mm × $10^{-2}$) | | | | | | | | |
| PR | 23.7 | 28.8 | 31.4 | 34.0 | 26.8 | 31.8 | 29.8 | 30.1 | 36.0 | 33.8 | 31.9 | 26.8 | 2.9 | 3.5 | 4.6 |
| SD | 27.8 | 28.1 | 31.5 | 32.1 | 38.2 | 35.5 | 35.6 | 34.0 | 32.7 | | | 36.6 | 1.9 | 3.6 | 5.2 |
| EG | 27.0 | 26.1 | 31.0 | 31.4 | 29.4 | 30.7 | 30.6 | 37.6 | 32.9 | | | 40.9 | 3.5 | 4.0 | 5.2 |
| LSD ($p = 0.05$) | 2.9 | 4.6 | 3.5 | 5.0 | 3.6 | 5.2 | 6.0 | 3.7 | 6.1 | | | 3.5 | | | |
| | | | | | | | No. of lateral buds/cm stem length | | | | | | | | |
| PR | 2.42 | 0.53 | 0.35 | 0.00 | 1.04 | 0.54 | 0.35 | 1.50 | 0.48 | 1.35 | 0.28 | 1.60 | 0.39 | 0.29 | 0.29 |
| SD | 1.99 | 0.99 | 0.63 | 0.37 | 1.22 | 0.68 | 0.38 | 1.49 | 0.94 | | | 1.52 | 0.19 | 0.26 | 0.30 |
| EG | 1.71 | 1.03 | 0.24 | 0.12 | 1.45 | 0.33 | 0.06 | 1.37 | 0.77 | | | 1.48 | 0.25 | 0.20 | 0.26 |
| LSD ($p = 0.05$) | 0.25 | 0.28 | 0.26 | 0.20 | 0.29 | 0.23 | 0.26 | 0.27 | 0.37 | | | 0.28 | | | |

NOTE: Values are means of 15 samples (except "half of stem winter killed," $n = 10$).
[a]For definitions see Fig. 1.
[b]A, terminal bud; B, subterminal bud; C, half-stem lateral bud; D, terminal bud on basal shoot.
[c]LSD ($p = 0.05$) for comparing means of shoots of similar points of origin from different pruning treatments.
[d]LSD ($p = 0.05$) for comparing means of shoots of different hardening regimes within columns.

compared with shoots of similar points of origin in the intact treatment, especially for EG seedlings.

*Number of lateral buds*

The number of lateral buds per unit of stem length for the intact treatment terminal shoots was significantly greater in PR than in SD seedlings (Table 1). In terminals of EG seedlings, fewer lateral buds per unit stem length formed than in either PR or SD seedlings. There were more lateral buds per unit stem length in the pruned treatments than in similar shoots of the intact treatment.

*Winter-damaged versus shoot-pruned seedlings*

Winter-damaged PR seedlings performed in much the same manner as seedlings in the shoot-pruned (HS) treatment. New leading shoot length was 4.88 cm in pruned seedlings compared with 4.77 cm in winter-damaged seedlings (Fig. 3). An average of 165 needles, with a stem unit length of 0.314 mm, was produced by new leading shoots of pruned seedlings, whereas new leaders of winter-damaged seedlings produced 137 needles at a stem unit length of 0.338 mm (Table 1).

## Discussion

Differences between the number of needle primordia predetermined in the 1st-year bud and the eventual number of needles on the 2nd-year shoot are attributed to free growth. Free growth accounted for similar averages of 118 needles in terminal shoots of EG seedlings, 110 needles in SD seedlings, and 128 needles in PR seedlings. In comparison, the percentage of free growth needles relative to needles from preformed needle primordia was distinctly different, i.e., 43, 73, and 187% for EG, SD, and PR seedlings, respectively. Pollard and Logan (1974) found that free growth in black spruce accounted for only 37% of the needles to form, while for white spruce and Engelmann spruce (*Picea glauca* (Moench) Voss and *Picea engelmannii* Parry, respectively), the proportion of free growth needles did not exceed 36% (Burdett *et al.* 1984). The capacity for free growth thus appears to be fixed by factors other than the degree of 1st-year bud development. If this is so, then free growth will neither add to, nor make up, differences in height growth as a result of 1st-year bud development.

Increased bud development appears to be a practical means of increasing spruce container seedling height growth following outplanting. In our greenhouse investigation, height growth by extended greenhouse culture seedlings was almost 6 cm greater than by production-run stock and, as a result, 2nd-year total height averaged 23.1 cm in EG seedlings compared with only 17.2 cm in PR seedlings. Improved bud development using extended greenhouse culture is one technique available to nurserymen for improving height growth to allow spruce container stock to more successfully compete with other vegetation following planting.

Increased terminal bud development resulted in both greater height growth and increased lateral bud production. Increases in the number of lateral buds should lead to greater rates of lateral shoot production, presumably increasing photosynthetic capacity and improving vigour and resulting in exponential increases in seedling growth.

While the absolute number of lateral buds was positively correlated with new shoot length and therefore with prior bud development, the number of lateral buds per unit of stem length increased in proportion to the amount of free growth, as, for instance, in a comparison of subterminal lateral buds in seedlings of the intact and TBR treatments.

Stem unit length was generally greatest in shoots from positions lower on the stem and in shoot-pruned seedlings. This may have been due to the greater proportion of free growth needles on these shoots as, according to Logan (1977), stem unit length of free growth needles exceeds that of predetermined needles. There was no apparent relationship between the number of needles and the stem unit length; in comparison, Kremer and Larson (1983) reported a negative correlation between these two factors.

Shoot pruning enhanced free growth in shoots at points lower on the stem, as shown by comparisons of the number of needles on lateral shoots produced by intact versus pruned seedlings. Basal shoots of intact PR seedlings produced only 29 needles, most or all of which can be assumed to have been predetermined; however, when base shoots became the new leaders because of pruning, an average of 169 needles were produced. Shoot pruning may have stimulated free growth by increasing the supply of root-originated gibberellins to the remaining apical meristems. Of the major classes of hormones, auxin and gibberellin are known to promote shoot elongation (Leopold and Kriedemann 1975). Of these, only the gibberellins are supposed to be transported from the roots to the shoots (Wareing 1981). Enhanced shoot elongation has been observed elsewhere following the application of exogenous gibberellin (Ross 1983). It can be postulated that the capacity for free growth is, at least in part, proportional to the supply to the shoots of gibberellins generated in the roots. Similarly, the rate of budbreak may also have been enhanced hormonally by shoot pruning. Both gibberellin (Lavender *et al.* 1973) and cytokinin (Wareing 1981) are transported acropetally from the roots to the shoots and have been implicated as playing roles in controlling the rate of bud flushing.

SD seedlings flushed more rapidly than seedlings that initiated buds at natural day lengths, a response noted by several authors (Dormling *et al.* 1968; Heide 1974; Sandvik 1980). However, the failure of PR seedlings to flush more rapidly than EG seedlings, despite greater chilling, and the slower flushing rate of PR seedlings compared with SD seedlings, despite the same chilling but the differing dates of bud initiation, indicates that the ability of seedlings to respond to chilling for dormancy relief depends upon the interaction between the stage of dormancy and bud development and the timing of exposure to chilling (Dormling *et al.* 1968; Campbell 1978; Sorenson and Campbell 1978; Lavender 1980).

Shoot growth characteristics of pruned seedlings were comparable to those of winter-damaged seedlings. New shoot length, number of needles on new shoots, and stem unit length were all similar in pruned and winter-damaged seedlings. Surviving buds were apparently unaffected, even though winter damage had killed other portions of the stem. Container seedlings produced for reforestation are in many cases culled if the terminal has been killed during overwintering. From our results, such culling appears unwarranted. Black spruce container seedlings in which the terminal buds only have been killed may reach a 2nd-year height within 2 cm of undamaged trees and other results have shown that with this degree of winter damage, root activity will not be reduced (Colombo and Glerum 1984). Culling is definitely warranted, however, when half the length of the stem is killed, as total 2nd-year height may be reduced by from 3 to as much as 7 cm compared with undamaged trees and root activity will be reduced by more than 60%.

In summary, increased terminal bud development resulted in

greater height growth, but only as a result of the expansion of stem units from predetermined needles. The capacity for free growth was apparently fixed independently of the degree of bud development. Free growth in lower stem shoots increased with the severity of shoot pruning, presumably because of a higher root:shoot ratio and perhaps an increased availability of gibberellins.

## Acknowledgements

This research was supported jointly by the governments of Canada and Ontario under the Forest Management Subsidiary Agreement (Project No. 585042). The technical assistance of K. D. Odlum and reviews by C. Glerum, D. C. F. Fayle, and D. Burger are gratefully acknowledged.

BURDETT, A. N., L. J. HERRING, and C. F. THOMPSON. 1984. Early growth of planted spruce. Can. J. For. Res. **14**: 644–651.

CAMPBELL, R. K. 1978. Regulation of bud-burst timing by temperature and photoregime during dormancy. Proc. North Am. For. Biol. Workshop, 5th. pp. 19–33.

CARLSON, L. W. 1983. Guidelines for rearing containerized tree seedlings in the Prairie provinces. Inf. Rep. NOR-X-214E, Can. North. For. Res. Cent.

COLOMBO, S. J. 1982. Winter damage to container seedlings: consequences and prevention. *In* Proceedings of the Ontario Ministry of Natural Resources Nurserymen's Meeting, June 10–12, 1982, Thunder Bay, Ont. Ontario Ministry of Natural Resources, Toronto, Ont. pp. 10–24.

——— 1984. Shoot morphology of winter-damaged black spruce container seedlings. Ont. Minist. Nat. Resour., For. Res. Note No. 36.

COLOMBO, S. J., and C. GLERUM. 1984. Winter injury to shoots as it affects root activity in black spruce container seedlings. Can. J. For. Res. **14**: 31–32.

COLOMBO, S. J., D. P. WEBB, and C. GLERUM. 1982. Cold hardiness and bud development under short days in black spruce and white spruce seedlings. *In* Proceedings, Canadian Containerized Tree Seedling Symposium, September 14–16, 1981, Toronto, Ont. *Edited by* J. B. Scarratt, C. Glerum, and C. A. Plexman. Can.–Ont. Jt. For. Comm. Symp. Proc. O-P-10. pp. 171–176.

DORMLING, I., A. GUSTAFSON, and D. VON WETTSTEIN. 1968. The experimental control of the life cycle in *Picea abies* (L.) Karst. I. Some basic experiments on the vegetative cycle. Silvae Genet. **17**: 44–64.

GROSS, H. L. 1983. Injuries to terminal shoots cause multiple-leadered nursery seedlings. Can. For. Serv. Inf. Rep. O-X-347.

HEIDE, O. M. 1974. Growth and dormancy in Norway spruce ecotypes. II. After-effects of photoperiod and temperature on growth and development in subsequent years. Physiol. Plant. **31**: 131–139.

JABLANCZY, A. 1971. Changes due to age in apical development in spruce and fir. Bi-Mon. Res. Notes Can. For. Serv. **27**(2): 10.

KREMER, A., and P. R. LARSON. 1983. Genetic control of height growth components in jack pine seedlings. For. Sci. **29**: 451–464.

LAVENDER, D. P. 1980. Effects of environment upon the shoot growth of woody plants. *In* Proceedings of the Joint Workshop of IUFRO Working Parties on Xylem and Shoot Growth Physiology, July, 1980, Fredericton, N.B. *Edited by* C. H. A. Little. Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, N.B. pp. 76–106.

LAVENDER, D. P., G. B. SWEET, J. B. ZAERR, and R. K. HERMANN. 1973. Spring shoot growth in Douglas-fir may be initiated by gibberellins exported from the roots. Science (Washington, D.C.), **182**: 838.

LEOPOLD, A. C., and P. C. KRIEDEMANN. 1975. Plant growth and development. 2nd ed. McGraw-Hill Inc., Toronto, Ont.

LOGAN, K. T. 1977. Photoperiodic induction of free growth in juvenile white spruce and black spruce. Bi-Mon. Res. Notes Can. For. Serv. **33**(4): 29–30.

POLLARD, D. F. W. 1973. Bud morphogenesis of white spruce *Picea glauca* seedlings in a uniform environment. Can. J. Bot. **52**: 1569–1571.

POLLARD, D. F. W., and K. T. LOGAN. 1974. The role of free growth in the differentiation of provenances of black spruce *Picea mariana* (Mill.) B.S.P. Can. J. For. Res. **4**: 308–311.

ROSS, S. D. 1983. Enhancement of shoot elongation in Douglas-fir by gibberellin $GA_{4/7}$ and its relation to the hormonal promotion of flowering. Can. J. For. Res. **13**: 986–994.

SANDVIK, M. 1980. Environmental control of winter stress tolerance and growth potential in seedlings of *Picea abies* (L.) Karst. N.Z. J. For. Sci. **10**: 97–104.

SORENSON, F. C., and R. K. CAMPBELL. 1978. Comparative roles of soil and air temperatures in the timing of spring budflush in seedling Douglas-fir. Can. J. Bot. **56**: 2307–2308.

WAREING, P. F. 1981. Root hormones and shoot growth. *In* Control of Shoot Growth in Trees, Proceedings of the Joint Workshop of IUFRO Working Parties on Xylem and Shoot Growth Physiology, July, 1980, Fredericton, N.B. *Edited by* C. H. A. Little. Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, N.B. pp. 237–256.